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Habitat and humans predict the distribution of juvenile and adult snapper (Sparidae: *Chrysophrys auratus*) along Australia's most populated coastline

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Ecosystem-based fisheries managers are increasingly seeking quantitative and spatially-explicit information on species distributions to assist with the management of fisheries and aquatic habitats. In this study, we used boosted regression trees (BRT) to build species distribution models for a highly valued coastal teleost – pink snapper (Sparidae: *Chrysophrys auratus*) across rocky reefs adjacent to Australia's most urbanised coastline. BRT models for juvenile (<25 cm total length) and adult (>32 cm total length) snapper were created using a suite of environmental and habitat predictors. A surrogate for multiple anthropogenic stressors, measured as surrounding human population density, was also included in the models. The BRT model for juvenile snapper performed well (cross-validated AUC = 0.78) and identified habitat features as the most important drivers of their distribution across the region. Juvenile snapper were commonly associated with small patch reefs of low relief adjacent to large estuarine water bodies. In contrast, the performance of the BRT model for adult snapper was weak (cross-validated AUC = 0.68) but identified human population density over habitat features as the strongest predictor of adult snapper distributions. Lower occurrences of adult snapper were associated with reef habitats adjacent to large metropolitan centres, suggesting anthropogenic stressors, such as water pollution, noise and fishing may be negatively impacting adult snapper in the region. Our results highlight essential habitats for snapper populations, notably the importance of large estuaries in the coastal seascape, which are nurseries for juvenile snapper. Knowledge of the demographic habitat associations and spatial distribution of snapper across this highly urbanised coastline will support ongoing management and monitoring of snapper populations and their key habitats.

1. Introduction

Detailed information on the spatial distribution of fishes and their essential habitats, such as nursery and spawning grounds is critical for effective ecosystem-based fisheries management (Valavanis et al., 2008). Species distribution models (SDMs) have become a powerful tool to describe species-habitat relationships and identify critical habitats for species' life-history processes in marine ecosystems (Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Leathwick et al., 2006). The ability of SDMs to reliably predict species distributions across unsampled locations may offer an opportunity to cost-effectively inform management over broad spatial scales (1–100's km) (Pittman et al., 2007). As a result, SDMs are becoming increasingly sought after by ecosystem-based fisheries managers (Moore et al., 2016). The utility of SDMs to produce maps of predicted species distributions also provides a visual means to engage key stakeholders, such as recreational and commercial fishers, in the management of a fishery.

Across temperate coastlines many studies have demonstrated strong environmental and habitat associations for demersal fishes. For example, previous research has shown that variation in depth (Bacheler et al., 2019; Malcolm et al., 2011; Williams et al., 2019); benthic substrata (Curley et al., 2002; Fulton et al., 2016; García-Charton and Pérez-Ruzafa, 2001; Guidetti, 2000; Young and Carr, 2015), habitat area (Rees et al., 2014), structural complexity (Pygas et al., 2020; Rees et al., 2018b; Young et al., 2010) and connectivity to estuaries and vegetated nursery habitats (Galaiduk et al., 2017; Rees et al., 2018a; Swadling et al., 2019) can have pronounced effects on the spatial distribution of temperate reef fishes. Despite demonstrating strong spatial patterns,

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much of this previous research has described temperate fish-habitat relationships without predicting species distributions beyond surveyed areas (Chatfield et al., 2010). In part, this is likely due to limited availability of broad-scale habitat data required to extrapolate spatial predictions. However, with greater access to remotely-sensed habitat information and tools to implement appropriate survey designs (Foster et al., 2020; Linklater et al., 2019; Lucieer et al., 2019) the opportunities to build SDMs for demersal temperate fishes are growing (Galaiduk et al., 2017; Monk et al., 2010; Young and Carr, 2015).

Globally, temperate regions are becoming increasingly affected by urbanisation and to some degree industrialisation (Diaz and Rosenberg, 2008; Lotze et al., 2006). Highly populated coastlines are likely to have a greater range and intensity of anthropogenic stressors (e.g. catchment development, water pollution, sedimentation, fishing and maritime activities) that place fish populations and their habitats under increased pressure (Todd et al., 2019). Not surprisingly, previous studies have identified substantial negative impacts of increasing human population density and human accessibility in marine environments on reef fish assemblages (Cinner et al., 2018; MacNeil et al., 2020; Stuart-Smith et al., 2008). Therefore, in highly urbanised and industrialised systems, SDMs for demersal fishes may benefit from including direct or indirect measures of anthropogenic stressors as these factors could be strong drivers of species distributions. Accounting for anthropogenic stressors in SDMs may also provide an opportunity to better understand and quantify potential effects of human disturbances on demersal fishes across relatively large spatial scales.

In this study, we develop SDMs for pink snapper (Sparidae: *Chrysophrys auratus*; hereafter referred to as snapper) on coastal reefs (15–45 m water depth) in the Greater Sydney region, New South Wales (NSW), Australia. This region extends from Stockton to Shellharbour and encompasses the large coastal cities of Sydney, Wollongong and Newcastle. As a coastal species, snapper have a high social value and are extremely important for the recreational and commercial fishing sector (West et al., 2015). Snapper are managed and assessed as a single east-coast biological stock along eastern Australia (Wortmann et al., 2018) and there is mounting evidence suggesting snapper stocks should be assessed and managed at local or regional scales (1–100's km scale) (Stewart et al., 2020). For example, previous research has indicated that the majority of snapper in eastern Australia are primarily resident, displaying spatially restricted movement patterns for substantial periods of time (Harasti et al., 2015a; Stewart et al., 2020; Sumpton et al., 2003) and are likely to recruit locally based on modelled larval projections (Roughan et al., 2011). Further, juvenile snapper use estuaries and shallow-water habitats as nurseries before migrating to deeper shelf waters (Curley et al., 2013; Parsons et al., 2014). Otolith chemistry has demonstrated that most offshore commercial catch of snapper in the Greater Sydney region originates from local estuaries (Gillanders, 2002). Consequently, spatially-explicit information on the distribution of snapper and their essential habitats over regional scales is likely to benefit the contemporary and future management of snapper populations. This is particularly pertinent in the Greater Sydney region, which covers Australia's most urbanised coastline with the greatest range and intensity of anthropogenic stressors of any regional coastline in Australia (Birch, 2000).

The aim of this study was to build species distribution models for juvenile and adult snapper on open coast rocky reefs within the Greater Sydney region. Two demographically-explicit models were developed for juveniles and adults as habitat associations are likely to differ between the life stages (Compton et al., 2012; Parsons et al., 2014). Snapper <25 cm and >32 cm total length were defined as juveniles and adults, respectively. These size classes were based on previous research finding ~60% of individuals at 32 cm and ~15% of individuals at 25 cm were mature in the central and southern coastal regions of NSW (Stewart et al., 2010). The probability of occurrence for the two life stages was modelled with various environmental and habitat predictors including neighbouring estuary area, reef area, depth, seafloor relief and the presence or absence of macroalgae and sponges. The effect of multiple anthropogenic stressors on snapper distributions were also examined using surrounding human population density as a surrogate measure (likely correlated to catchment development, water pollution, sedimentation, fishing and maritime activities). Model outputs were extrapolated across mapped rocky reefs in the Greater Sydney region to produce predictive maps of juvenile and adult occurrence. Development of SDMs and predicted distribution maps provides a supplementary tool to support ecosystem-based fisheries management of the snapper fishery and importantly, provides a template for their application to other fisheries.

2. Materials and methods

2.1. Study region

The study was completed in the Greater Sydney region, which is situated in central NSW, Australia and covers approximately 350 km of coastline and extends offshore to 3 nautical miles from Stockton to Shellharbour (Fig. 1). The region comprises the highest coastal population density in Australia, including NSW's three largest cities - Sydney, Wollongong and Newcastle, which as of 2016, had populations of 4.8, 0.2 and 0.15 million people, respectively (Australian Bureau of Statistics, 2017). Between these three major metropolitan areas are terrestrial National Parks and coastal towns resulting in high variation of human population densities throughout the region. Seabed type mapping has been done for approximately 62% of marine waters between 0 and 60 m in the region using a range of methods including multibeam sonar (https://portal.aodn.org.au), LiDAR (https://elevation.fsdf.org.au), side scan sonar and aerial photography (Gordon and Hoffman, 1989; Jordan et al., 2010; Kinsela et al., 2020; Linklater et al., 2019). Seabed mapping of the region has revealed extensive rocky reef habitat between depths of 20 and 40 m – the target habitat for this study.

2.2. Sampling design

To survey snapper populations representatively across the Greater Sydney region, spatially balanced sampling designs were created using the 'MBHdesign' package in R (Foster et al., 2020). Survey sites were restricted to rocky reef habitat between depths of 20 and 40 m to align with data from the surrounding NSW coastline (Knott et al., 2021). Given estuaries are important nursery grounds for snapper and often a direct sink for catchment derived contamination and its discharge into open coastal environments, we added unequal inclusion probabilities to the spatially balanced designs to ensure rocky reef sites across a gradient of distances to estuaries were selected. Further sampling design details are in Appendix A.

2.3. Underwater video sampling

Juvenile and adult snapper occurrences were surveyed using baited remote underwater stereo-video systems (stereo-BRUVs; Langlois et al., 2020) baited with ~500 g of fresh chopped pilchards (*Sardinops sagax*). Sampling was done in the Austral winter and spring of 2019 between the months of June and October. At each site, one stereo-BRUVs was deployed on the seafloor for a minimum of 35 min to achieve a 30 min sample. Previous research has shown that a 30 min sample is adequate to representatively survey temperate reef fish assemblages on the east coast of Australia (Harasti et al., 2015b). Each stereo-BRUVs was constructed as per Malcolm et al. (2007), which included a galvanized metal frame containing a video camera (SONY ×3000 or digital Canon HG21) pointed at a bait bag mounted horizontally at the end of a 1.5 m long bait arm. Cameras were housed within high-pressure polyvinyl chloride pipe with flat acrylic endports yielding a field of view of 110°. Prior to, and during the sampling campaign, stereo-BRUVs were calibrated using the software CAL (SeaGIS, seagis.com.au) following the 3D calibration

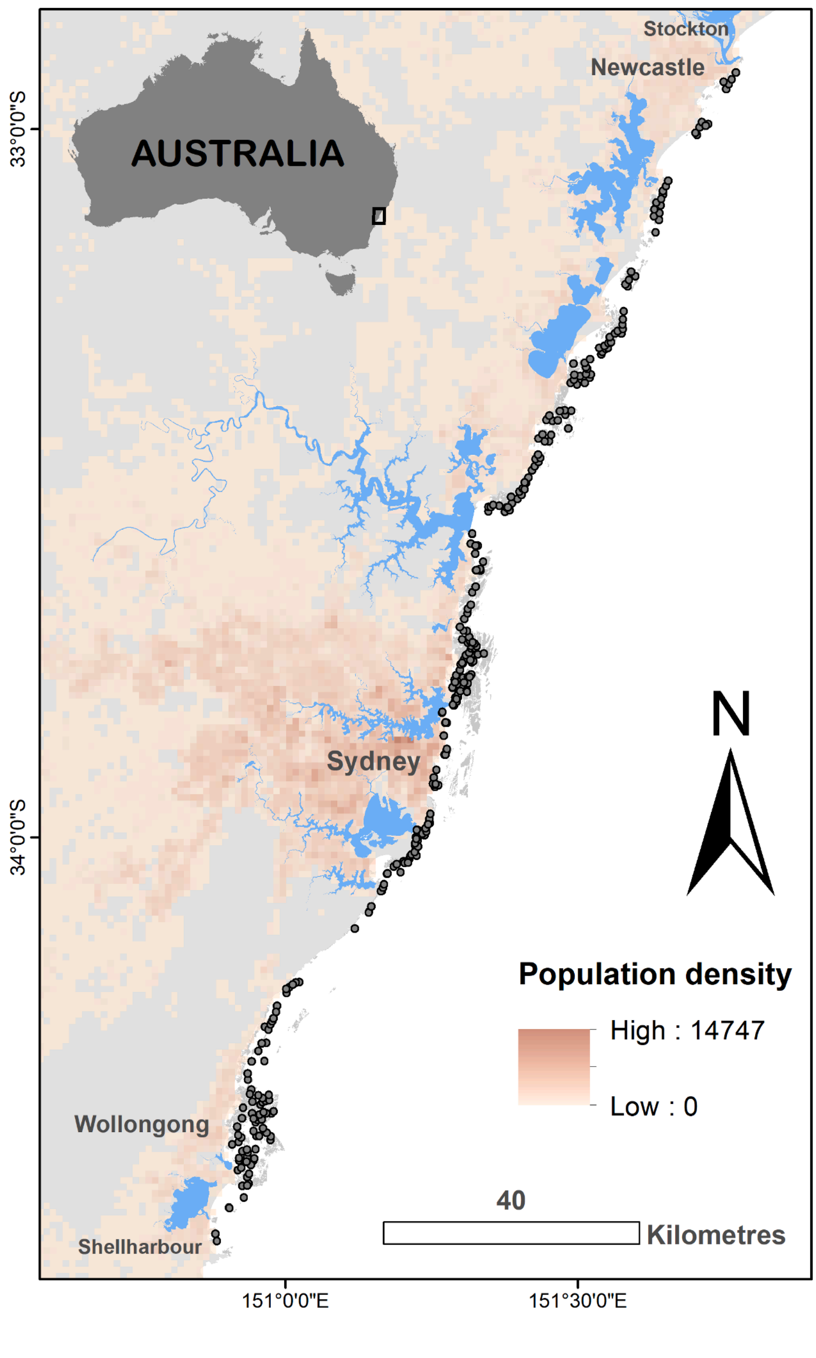

Fig. 1. Position of the 308 successful stereo baited remote underwater video station deployments (grey circles) in the Greater Sydney region on rocky reef habitat between depths of 15 and 45 m. Overlaid grid represents population per km^2 with darker regions containing a greater population density than lighter regions. Blue areas represent open estuarine waters. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

procedure outlined by Boutros et al. (2015) to accurately measure snapper lengths, estimate water clarity and standardise the area surveyed (Langlois et al., 2020). As stereo-BRUVs had a camera separation of 800 mm and a convergence angle of 8°, length measurements of juvenile and adult snapper observed during the study were likely to have a high accuracy (±5% error) (Gardner et al., 2021). Of the 350 stereo-BRUVs deployed, 308 had unobstructed field of views in both cameras enabling length measurements.

2.4. Video analysis

Videos of 30 min duration were annotated using EventMeasure software (SeaGIS, seagis.com.au) and a standardised field of view of 5 m distance from the centre of the cameras. For each replicate stereo-BRUVs deployment, we recorded snapper MaxN, which was the maximum number of snapper individuals in any frame at any point in time (Parker and DeMartini, 1995). At time of MaxN the individual fork lengths of each snapper were measured. Data were extracted from EventMeasure software and checked following Langlois (2017). Fork length measurements were converted to total lengths following formula outlined in Ferrell and Sumpton (1997) and recoded to presences or absences of juvenile (<25 cm total length) and adult snapper (>32 cm total length) for each deployment based on Stewart et al. (2010).

2.5. Explanatory variables

A number of habitat and environmental variables were included in the analysis which were either recorded *in situ*, from stereo-BRUVs footage or in a Geographic Information System using remotely-sensed environmental data (Table A.1). Fine-scale habitat features and vertical relief of each site were analysed in the program TransectMeasure (SeaGIS, seagis.com.au) following the method described in McLean et al. (2016). A 5 × 4 grid was overlaid on a high definition still frame for each stereo-BRUVs deployment splitting the image into 20 cells. The dominant habitat type and vertical relief was then scored for each cell following the CATAMI classification scheme (Althaus et al., 2015). Habitat types included consolidated (rocky reef), unconsolidated (sand/rubble), macroalgae, sponges and ascidians. For each cell over benthos an estimate of vertical relief was scored between 0 and 5 following Wilson et al. (2007). Data were exported from TransectMeasure software and checked and manipulated using R scripts available from Langlois (2017). Cells of open water were removed before calculating a mean estimate for habitat type percentage cover and vertical relief for each deployment. Depth was recorded *in situ* using the research vessel sounder at each survey site. Maximum visibility was also quantified for each deployment by making a 3D point measurement of the furthest identifiable object (for example, substrate, alga and fish) in EventMeasure at the maximum range of visibility (Goetze et al., 2019). Deployments in areas of greater water clarity and with unobstructed field of views resulted in larger maximum visibility measurements. Maximum visibility was included as a potential model covariate as variation in visibility among deployments could possibly influence the detectability of snapper.

To quantify the surrounding seascape characteristics of each survey site, a range of broad-scale environmental and anthropogenic predictors were calculated. Using a spatial layer of rocky reef habitat throughout the Greater Sydney region derived from previously collected singlebeam and multibeam survey data (Gordon and Hoffman, 1989; Jordan et al., 2010), surrounding reef area was calculated for each deployment using 50 m, 100 m, 200 m, and 500 m radii buffers in ArcGIS (ESRI, 2011). Following a similar procedure, surrounding area of open estuaries in the Greater Sydney region was calculated for each deployment using buffers with a radius of 10 km and 20 km. Surrounding human population density for each deployment was calculated from Australian Bureau of Statistics Australian Population Grid 2016 (Australian Bureau of Statistics, 2017) within circular buffers of 10 km and 20 km radius using zonal statistics function in R. Human population density was included in the species distribution models as a surrogate for multiple anthropogenic stressors, where greater population density is likely correlated to catchment development, water pollution, sedimentation and maritime activities. Human population density is also an appropriate surrogate for fishing effort and accessibility as distance to nearest boat ramp was correlated with human population density. No oceanographic variables, such as sea surface temperature, were included as model predictors as the study was completed within a bioregion where there is relatively limited broad-scale oceanographic variability. For example, during the study the mean difference in sea surface temperature between the northern and southern survey sites was 0.44 °C calculated from the satellite derived IMOS - SRS - SST - L3S – Single Sensor - 6 day - day and night time measurements (www.aodn.org.au).

Table 1
Summary of the optimal parameters and predictive performance measures for the juvenile and adult snapper BRT models, tc = tree complexity, nt = number of trees, lr = learning rate, AUC = Area Under the receiver operating Curve and TSS = True Skill Statistic.

Model	tc	nt	lr	Cross-validation		Test with independent data	
				AUC	R^2	AUC	TSS
Juvenile	2	1700	0.003	0.78	15.3	0.81	0.39
Adult	2	1200	0.001	0.67	5.69	0.50	–

2.6. Preliminary data exploration

Prior to modelling, data exploration was performed to examine potential outliers, homogeneity and collinearity of explanatory variables. The habitat types; macroalgae and sponges were converted to presence or absence due to their highly skewed distribution in percentage cover. Further, the consolidated and unconsolidated habitat types were removed due to their strong collinearity and skewed distributions. Reef area calculated at 50 m, 100 m, and 200 m radii scales were heavily right skewed with a large proportion of sites having a 100% reef cover in the surrounding seascape. As a result, only the 500 m radius scale of reef area was included for further analysis. Square root transformations of the human population density predictors, estuary area predictors and reef area (500 m) were performed to improve homogeneity. For each of the explanatory variables calculated at multiple spatial scales (human population density and estuary area), only one was included for further analysis, which was determined by visual inspection of plotted relationships. The final subset of continuous explanatory variables had Pearson's correlation coefficients of less than 0.2.

2.7. Model formulation and evaluation

To assess the relative importance of habitat, environmental and anthropogenic variables on the spatial distribution of juvenile and adult snapper we used boosted regression trees (BRT). BRTs were chosen over other approaches as they are a flexible modelling approach that can model non-linear relationships, incorporate numerous data types and provide robust spatial predictions (Elith et al., 2008). BRT models were performed on presence/absence data for juvenile and adult snapper with a Bernoulli error distribution and a logit link function using the "gbm" package version 2.1.5 (Greenwell et al., 2018) in R using code adapted from Elith et al. (2008). We modelled the presence/absence of snapper rather than the MaxN or relative biomass due to the high proportion of zeros in the juvenile and adult response measures. Due to our sample size, models were developed using 5-fold cross-validation where the learning-rate, tree complexity and bag-fraction settings were optimised to build models containing between 1000 and 2500 trees and best all-round performance. The "gbm.simplify" function was used to reduce the number of variables by an iterative backwards stepwise removal of the least influential variables using 5-fold cross-validation until the change in predictive deviance was minimised. Partial plots of predictors in each of the final models were plotted using the "ggplot2" package (Wickham, 2016) and "ggBRT" package (Jouffray et al., 2019), where bootstrapping was used to calculate 95% confidence intervals. Model performance for each juvenile and adult snapper was evaluated on the portion of the training data withheld for cross-validation during model building. The cross-validated Area Under the receiver operating Curve (AUC) was used to assess model performance, which quantifies the ability of the model to discriminate between presences and absences in the dataset (Franklin, 2010). AUC values range from 0 to 1, where >0.9 indicate excellent model performance, 0.7–0.9 moderate to high performance, 0.5–0.7 low performance and <0.5 indicates performance was no better than random. Percent deviance explained by each model was also used as a measure of overall model goodness-of-fit, which was calculated as (1 – (cross-validated deviance/mean total deviance)). Spatial autocorrelation in model residuals was assessed using spline correlograms (BjØrnstad and Falck, 2001), which indicated that there was limited evidence of spatial autocorrelation for both models

(Fig. A.2).

Model performance was also evaluated using an independent stereo-BRUVs dataset collected in the adjoining Batemans Marine Bioregion to the south of the Greater Sydney region between Kiama (34.6738° S, 150.8444° E) and Ulladulla (35.3572° S, 150.4613° E) in 2015 and 2016 (Fig. A.5). These data were collected by NSW Department of Primary Industries Fisheries Research as part of the state-wide monitoring of rocky reef fishes (Knott et al., 2021) and were accessed from the Global Archive repository (https://globalarchive.org/). Fine-scale habitat and seascape variables were calculated for each deployment as described above. Estimates of reef area was derived from a rocky reef shapefile digitised from NSW Multibeam Surveys (AODN https://portal.aodn.org.au) and NSW marine LiDAR (Geosciences Australia https://elevation.fsdf.org.au/) data (Jordan et al., 2010). Deployments in the independent data set ranged from 14 km to 100 km south of the most southern survey site in the Greater Sydney region. To evaluate the Greater Sydney region models with independent data, confusion matrices were run to calculate two model accuracy indices, AUC and true skill statistic (TSS). To calculate the TSS, the predicted probability of occurrence values (0–1) were converted into categories of suitable and unsuitable localities using

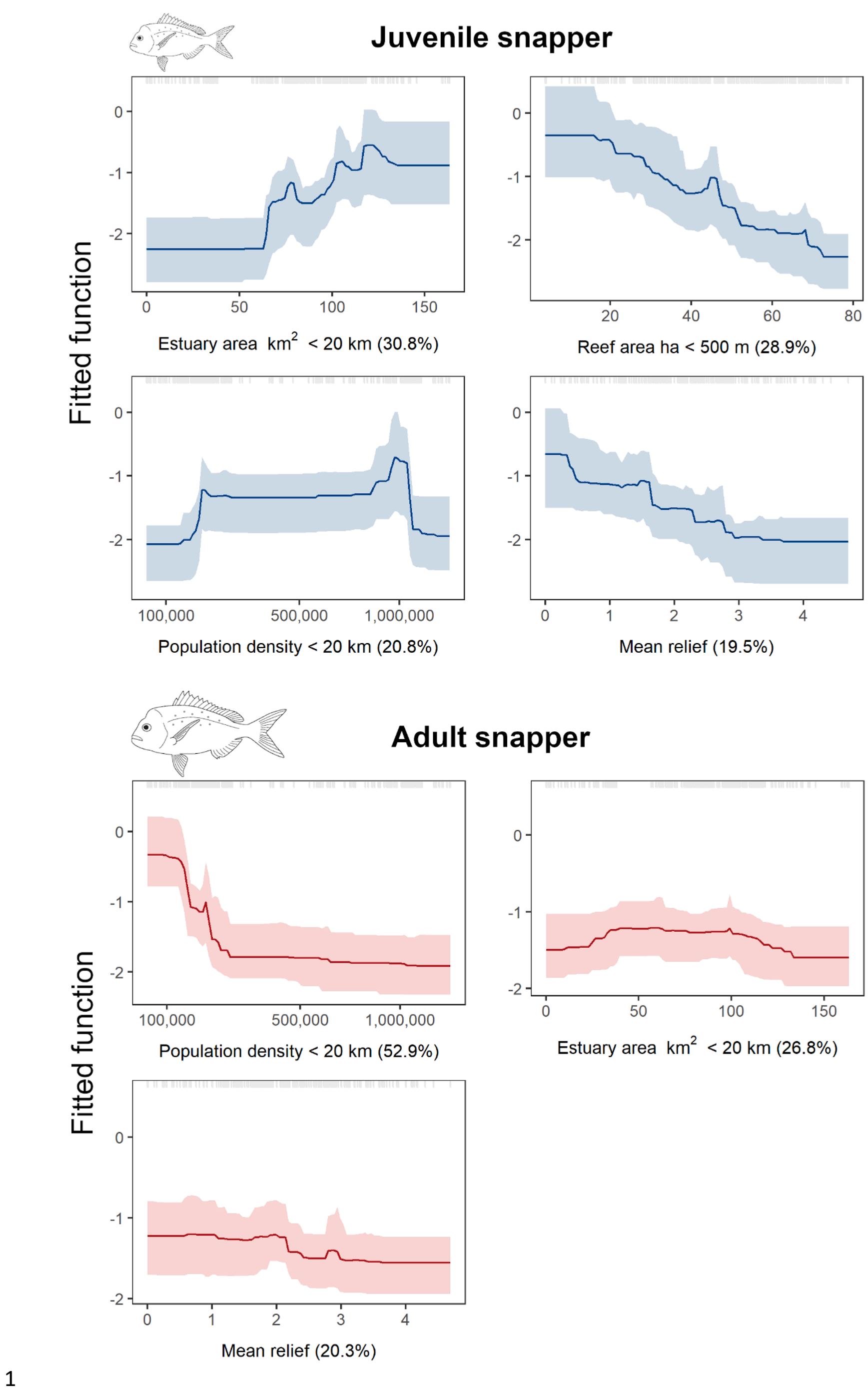

Fig. 2. Partial dependency plots with 95% confidence intervals for the most influential variables in the juvenile and adult snapper models. The plots show the effect of a given predictor on the probability of occurrence of juvenile and adult snapper while keeping all other variables at their mean. The relative importance of each predictor variable within the BRT model is shown in brackets next to the variable name. Grey rugs along the top of each plot indicate observed data points.

a threshold of 0.5. All predicted probabilities of occurrence for adult snapper were <0.5 and therefore, TSS was only calculated for juvenile snapper. The TSS ranges from −1 to 1, where 0 denotes the threshold between models with some predictive skill (model skill increases towards 1) and models that are no better than random (model skill declines towards −1) (Allouche et al., 2006). To further validate the juvenile and adult models, we plotted the distribution of observed occurrences in the independent data set across the range of predicted probabilities of occurrence derived from the Greater Sydney region models. A high count of observed occurrences at sites of greater suitability would indicate that the models are a valuable decision-support tool.

2.8. Spatial predictions

Maps of the predicted probability of occurrence of juvenile and adult snapper throughout the Greater Sydney region were generated following the general procedures of Leathwick et al. (2006) and Hill et al. (2014). Firstly, a fish net layer was created in ArcGIS (ESRI, 2011), where points were separated by 500 m and clipped to the rocky reef shapefile used for creating the spatially balanced design. For each point, explanatory variables included in the optimal BRT models were calculated following procedures outlined above. Fine-scale variables from stereo-BRUVs imagery that could not be estimated for each fish net point (for example, mean relief) were kept at their mean value. The optimal BRT models were fitted to a bootstrap sample of the fish net points, which was then used to make predictions across the spatial extent of rocky reef in the region. This procedure was repeated 1000 times to generate 1000 spatial layers of predicted probabilities of juvenile and adult snapper occurrences. The mean probability of occurrence and its standard deviation was generated for each point and converted to a raster layer. Maps of the mean predicted probabilities of occurrence and associated error were generated for juvenile and adult snapper.

3. Results

Juvenile snapper (<25 cm total length) and adult snapper (>32 cm total length) were recorded on 72 and 71 of the 308 stereo-BRUVS deployments across the Greater Sydney region, respectively. The BRT model for juvenile snapper performed moderately well (cross-validated AUC 0.78) explaining 15.3% of the variation in their occurrence in the region (Table 1). Habitat and seascape variables were the most important predictors of juvenile snapper occurrence with a combined relative influence of 79% within the BRT model (Fig. 2). Juvenile snapper preferred small patch reefs with low relief adjacent to large estuarine water bodies (Fig. 2). A higher probability of juvenile occurrence was also observed with increasing population density within 20 km until approximately 1,000,000 people where occurrence sharply declined. Model validation against an independent data set revealed that the optimal juvenile snapper model performed well (AUC = 0.80, TSS = 0.31), indicating that habitat associations and spatial predictions are reliable for management purposes. Furthermore, a high count of occurrences in the independent data set were observed at sites of greater predicted suitability (Fig. A.4).

The BRT model for adult snapper had relatively poor performance (cross-validated AUC 0.68) explaining only 5.7% of the variation in their occurrence (Table 1). In contrast to juvenile snapper, population density was a much more important predictor of adult snapper than habitat and seascape variables, accounting for over half (52.9%) of the total variation explained by the BRT model (Fig. 2). The seascape and habitat variables, surrounding estuary area and mean relief had a relative influence of 26.8% and 20.3% respectively, however, these relationships were relatively weak. Higher probabilities of adult snapper occurrence were associated with population densities less than 150,000 people within 20 km. Probability of occurrence dropped substantially between population densities of 150,000 to 300,000 people within 20 km where it continued to remain low with increasing population density (Fig. 2). Validation of the optimal adult snapper model against an independent data set was poor (AUC = 0.51) although a positive trend between predicted suitability and adult snapper occurrences across the independent data set was observed (Fig. A.4).

Predicted species distributions of juvenile and adult snapper from the optimal BRT models showed a high degree of spatial variation across the Greater Sydney region (Fig. 3). Hotspot locations for juvenile snapper were strongly associated with seascapes characterised by patchy reef systems in close proximity to large estuarine water bodies. Important locations included reefs in the northern section of the Greater Sydney region and adjacent to the Hawkesbury River and Port Hacking. Higher occurrences of adult snapper were predicted along remoter coastlines of the region with low population densities, which were generally adjacent to terrestrial National Parks. Spatial variation in the error surrounding predictions were generally positively related to predicted probability of occurrences (Fig. A.3).

4. Discussion

Identifying important habitats and understanding how they shape the spatial distribution of targeted fishes is valuable for effective ecosystem-based fisheries management (Moore et al., 2016; Valavanis et al., 2008). In this study, a BRT modelling approach was used to assess habitat preferences as well as the influence of anthropogenic pressures on the distribution of snapper on open coast rocky reefs across Australia's most densely populated coastline. The occurrence of juvenile snapper (<25 cm total length) in the region was driven largely by habitat and seascape features, with juveniles preferring small patch reefs of low structural complexity in close proximity to large estuarine water bodies. In contrast, habitat and seascape variables were poor predictors of adult snapper occurrence (>32 cm total length). Rather, adult snapper were observed more frequently in the remoter areas of the region where surrounding human population density was relatively low. These findings confirm other research highlighting the importance of modelling habitat associations for snapper at different life stages (Compton et al., 2012; Galaiduk et al., 2017; Swadling et al., in review).

The overwhelming influence of habitat and seascape variables in explaining the occurrence of juvenile snapper is not surprising considering the species' life history. Snapper often recruit into estuaries, bays and shallow-water inlets where they use these systems as nursery habitats before migrating to the open coast (Curley et al., 2013; Gillanders, 2002; Parsons et al., 2014). Expectedly, the area of surrounding estuary within a 20-km seascape was one of the most important drivers of juvenile snapper distributions, with higher occurrences observed on open coast reefs adjacent to large open estuaries. This finding supports those by Swadling et al., (in review) who recorded a higher abundance and smaller size class of snapper on coastal reefs within 10 km of estuary entrances in the neighbouring Batemans Marine Bioregion. Juvenile snapper were also strongly associated with seascapes dominated by small patch reefs of relatively low structural complexity. Laboratory experiments have demonstrated that juvenile snapper choose sheltered habitat when exposed to a predatory threat, yet field research indicates they are most abundant over soft sediments adjacent to rocky reef (Ross et al., 2007). Therefore, a likely explanation for our results is that juvenile snapper prefer reef-sand boundaries as these edges provide food resources (Langlois et al., 2005) and the presence of reef may act as shelter to assist predator avoidance. In contrast to juveniles, only weak habitat and seascape associations were observed for adult snapper across the region. This finding aligns with that of Swadling et al., (in review), who found habitat variables, such as distance to estuary, estuary area and depth to be poor predictors of adult snapper with their distribution being relatively even on open coast reefs between depths of 20–40 m in southern NSW.

Human population density was the strongest predictor of adult snapper in the region, where substantially lower occurrences were

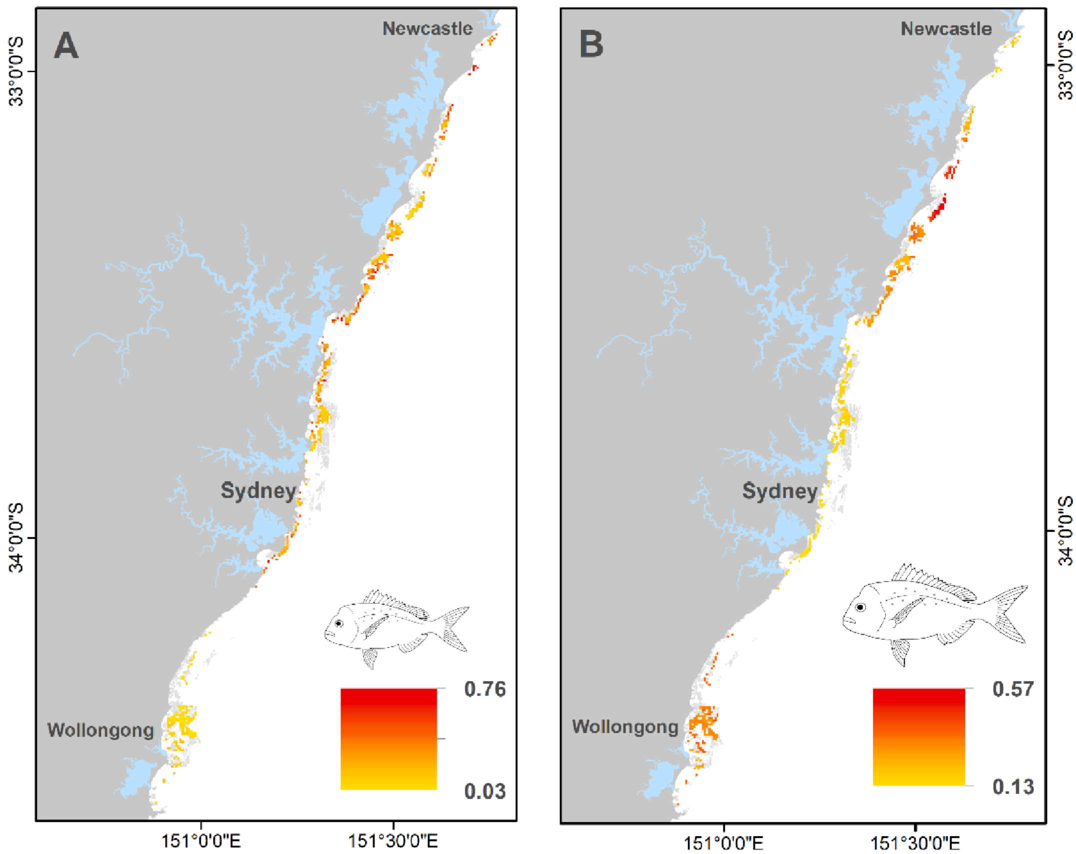

Fig. 3. Maps of the predicted probability of occurrence of A) juvenile and B) adult snapper across rocky reefs between depths of 20 and 40 m in the Greater Sydney region, NSW, Australia.

observed on reefs adjacent to population centres with more than 150,000 people within 20 km. A number of previous studies have also demonstrated negative impacts of greater surrounding human population density and human accessibility to reef fish assemblages (Cinner et al., 2018; MacNeil et al., 2020; Mora et al., 2011; Stuart-Smith et al., 2008). Similarly, in Western Australia, Navarro et al. (2020) observed lower recreational catches of dhufish, a targeted demersal fish in waters surrounding the Perth metropolitan area relative to regional coastal areas in the State. Many anthropogenic stressors associated with high population densities in the Greater Sydney region could be driving the negative association with adult snapper. For example, the highly urbanised and industrialised coastlines of the region's three major cities experience elevated levels of pollution, maritime industries and catchment development (Birch, 2000) possibly leading to reductions in adult snapper occurrence. However, as juvenile snapper did not display a clear negative relationship with increasing human population density and are protected from harvesting by a minimum legal size limit (NSW Fisheries Management Act, 1994), our results suggest fishing may be the responsible driver of adult snapper distributions in the region. However, given the relatively poor performance of the adult snapper model, further research is required to better assess whether fishing is the predominant anthropogenic stressor influencing adult snapper distributions in the region. Future studies could test fishing related hypotheses by including spatially-explicit measures of recreational and commercial fishing effort in species distribution models (Griffin et al., 2020; Navarro et al., 2020) or by using manipulative experimental approaches.

Spatial predictions of the distribution of juvenile and adult snapper showed a number of hotspots in their occurrence throughout the Greater Sydney region. Generally, three important locations were identified for juvenile snapper, which were seascapes characterised by patchy reef systems in close proximity to large estuarine water bodies. Hotspots for juvenile snapper included reefs between Newcastle (32.93° S, 151.78° E) and Lake Macquarie (33.03° S, 151.56° E), Terrigal (33.45° S, 151.44° E) and the Hawkesbury River (33.53° S, 151.24° E) and reefs adjacent to Port Hacking (34.07° S, 151.12° E) in southern Sydney. As human population density was the primary driver of the spatial distribution of adult snapper, higher frequencies of occurrence were predicted along the region's more remote coastlines. These locations were generally adjacent to terrestrial National Parks, including the northern Illawarra and southern Sydney coastlines surrounding the Royal National Park (34.14° S, 151.12° E), the Bouddi National Park (33.52° S, 151.39° E) and the National Parks and conservation areas surrounding Norah Head (33.28° S, 151.57° E) in the north of the region.

Identifying habitat associations and important locations for juvenile and adult snapper has a number of implications for their management in the region and temperate Australian coastlines. Firstly, our results indicate that large open estuaries are important nursery habitats for snapper in the Greater Sydney region, as higher occurrences of juvenile snapper were recorded on reefs adjacent to these systems. Similarly, using otoliths Gillanders (2002) found that most snapper (89%) caught in the region's commercial fishery originated from local estuaries. Together, these findings suggest that local estuaries play a major role in supplying individuals to the region's open coast environment. Furthermore, as snapper can display restricted movement patterns in open coast environments (Harasti et al., 2015a; Stewart et al., 2020; Sumpton et al., 2003) with modelling suggesting limited larval dispersal capabilities (Roughan et al., 2011), there is a growing consensus that management across regional scales may be required to sustain local fisheries (Stewart et al., 2020). Consequently, it is important that the condition of estuaries, including their vegetated habitats (seagrass and saltmarsh) and water quality are maintained or enhanced to ensure recruitment of juveniles to the open coast snapper population. Management initiatives aimed at improving the health of estuaries and their resilience to increasing and ongoing anthropogenic pressures are likely to benefit the region's snapper population.

The predictive performance of the optimal models evaluated using an independent data set varied greatly between juvenile and adult snapper. The optimal juvenile snapper model had a relatively high degree of transferability, predicting the occurrences of juvenile snapper in the neighbouring northern section of Batemans Marine Bioregion relatively well. In contrast, the optimal model for adult snapper had poor transferability. However, for both juvenile and adult snapper, a positive trend was observed between predicted suitability and observed occurrences in the independent data set suggesting model outputs are useful for management purposes. It is important to acknowledge that our Greater Sydney region models have a temporal limitation as samples were collected in Austral winter and early spring. We encourage future repeat baited remote underwater video sampling in the region to further assess model performance and quantify temporal variation in snapper distributions, which has been shown to vary among seasons and years (Egli and Babcock, 2004; Malcolm et al., 2015).

5. Conclusions

Globally, coastal ecosystems are becoming increasingly urbanised, leading to a greater range and intensity of human pressures on important fisheries species and nearshore habitats (Todd et al., 2019). Consequently, information on the spatial distributions, critical habitats, and impacts of multiple human stressors on target species is valuable to assist ecosystem-based fisheries management in urbanised environments. In this study we demonstrated the use of BRTs in assessing the habitat associations and effect of multiple human stressors on the distribution of a species of significant socio-economic value along Australia's most densely populated coastline. We showed a strong relationship between juvenile snapper, estuaries, and adjacent low relief nearshore habitat, emphasising the importance of preserving these habitats for the ongoing recruitment of this species. In contrast, adult snapper did not share strong habitat associations. Rather their distribution was negatively related to surrounding human population density, suggesting impacts in their occurrence due to multiple human threats. Our study provides a clear example on the application of demographically-explicit species distribution models to assess human pressures and habitat associations for an important fisheries species. This information can be used to support effective ecosystem-based management of important fisheries species.

Author statement

M.J. Rees: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Roles/Writing - original draft; Writing - review & editing. N.A. Knott: Conceptualization; Data curation; Investigation; Methodology; Project administration; Resources; Supervision; Roles/Writing - original draft; Writing - review & editing. M.L. Hing: Data Curation; Investigation; Methodology; Resources; Writing - review & editing. M. Hammond: Data Curation; Investigation; Methodology; Resources; Writing - review & editing. J. Williams: Data Curation; Investigation; Resources; Writing - review & editing. J. Neilson: Data Curation; Investigation; Resources; Writing - review & editing. D.S. Swadling: Data Curation; Investigation; Writing - review & editing. A. Jordan: Conceptualization; Funding acquisition; Project administration; Resources; Supervision; Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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APPENDIX A

To survey snapper populations representatively across the Greater Sydney region, spatially balanced designs were created following Foster et al. (2020). Survey sites were restricted to rocky reef habitat between depths of 20 and 40 m to align with data from the surrounding NSW coastline (Knott et al., 2021). Given estuaries are important nursery grounds for snapper and often a direct sink for catchment derived contamination and its discharge into open coastal environments, we added unequal inclusion probabilities to the spatially balanced designs to ensure rocky reef sites across a gradient of distances to estuaries were selected. This was achieved by creating a distance from major estuary layer using the Euclidian Distance tool in ArcGIS (ESRI, 2011), for each of the major estuaries in the region (permanently open estuaries: Hunter River, Lake Macquarie, Tuggerah Lake, Hawkesbury River, Port Jackson, Botany Bay, Port Hacking, Port Kembla and Lake Illawarra). The distance from major estuary layer was clipped to a shapefile of rocky reef habitat between 20 and 40 m in depth, which represented the potential survey area for the region (Fig. A.1). As rocky reef between 20 and 40 m within the Greater Sydney region generally exists as a long narrow belt running parallel to the coastline the region was separated into 5 subregions based on natural breaks in reef habitat; i) Port Kembla to Bellambi, ii) Coal Coast, iii) Royal National Park to Long Reef, iv) Long Reef to Avoca and, v) Avoca to Newcastle. For each subregion, a spatially balanced design with biased inclusion probabilities was created in R statistical computing language (R Core Team, 2020) using the 'MBHdesign' package (Foster et al., 2020) with the number of 'distance bins' set to 4. The density of sites among subregions was kept consistent at approximately 1 site per square kilometre of rocky reef. The spatial layout of the sites was then reviewed to ensure sites were separated by a minimum of 250 m. Occasionally, sites were within 250 m of one another and in these instances one site was re-positioned to achieve the minimum distance of separation. In total 350 sites were allocated across the Greater Sydney region.

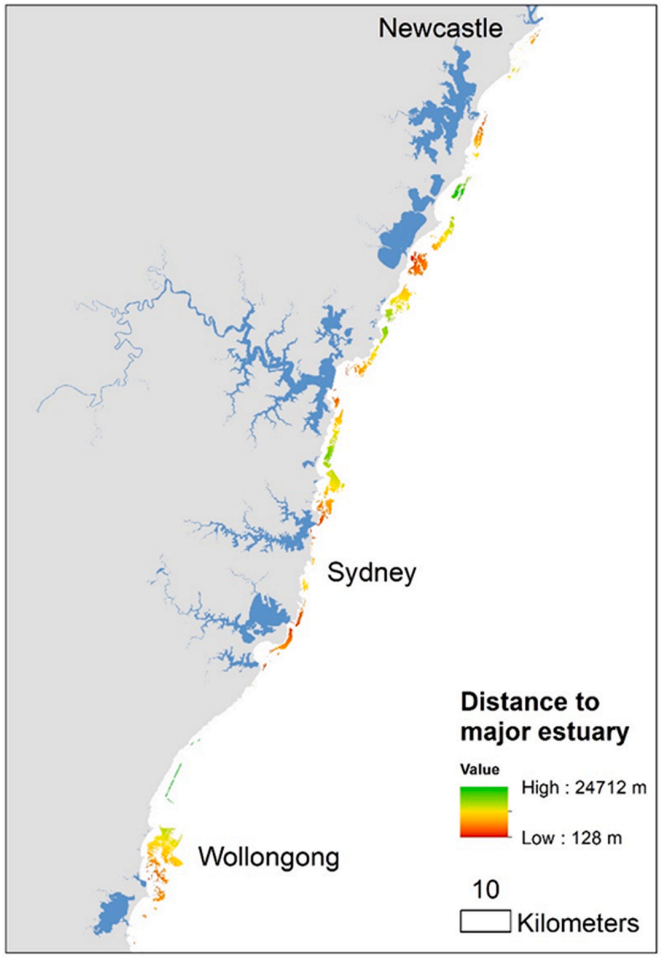

Fig. A.1. Proximity of deep rocky reef habitat (20–40 m) to estuaries within the Greater Sydney region. Colour gradient represents distance from the entrance of the nearest permanently open major estuary. The raster layer was included in the spatially balanced design to create unequal inclusion probabilities to favour site selections close to open estuaries.

Table A.1
Details of the explanatory variables used to model the distribution of snapper with boosted regression trees.

Predictor	Description and calculation	References
Habitat/Seascape		
Estuary area	Area of estuarine water within a 10 km and 20 km buffer of each survey site (ArcGIS - ESRI, 2011).	Gillanders (2002); Swadling et al., (in review)
Reef area	Area of rocky reef within a 50 m, 100m, 200m and 500 m buffer of each survey site (ArcGIS - ESRI, 2011).	Ross et al. (2007); Rees et al. (2014); Swadling et al. (2019)
Macroalgae presence/ absence	Presence or absence of macroalgae on BRUVs footage recorded at each survey site following McLean et al. (2016) in Transect Measure (SeaGIS, seagis.com.au).	Fulton et al. (2016); Curley et al. (2002)
Sponge presence/ absence	Presence or absence of sponges on BRUVs footage recorded at each survey site following McLean et al. (2016) in Transect Measure (SeaGIS, seagis.com.au).	Choat and Ayling (1987); Curley et al. (2002)
Depth	Bathymetry of survey site recorded *in situ* using depth sounder.	Williams et al. (2019); Rees et al. (2014); Parsons et al. (2016)
Relief	Mean relief score recorded from BRUVs footage at each survey site following definitions of (Wilson et al., 2007). Quantified in Transect Measure (SeaGIS, seagis.com.au) following procedures of McLean et al. (2016).	Rees et al. (2018b); Pygas et al. (2020)
Visibility	Maximum distance of the furthest object (benthic substrate or fish) in the stereo cameras field of view measured in EventMeasure (SeaGIS, seagis.com.au).	Bacheler et al. (2019)
Anthropogenic stressors		
Human population density	Sum of the number of people that reside within a 10 km and 20 km radius buffer surrounding each survey. Calculated from the Australian Population Grid 2016 (Australian Bureau of Statistics, 2017) in R using zonal statistics.	

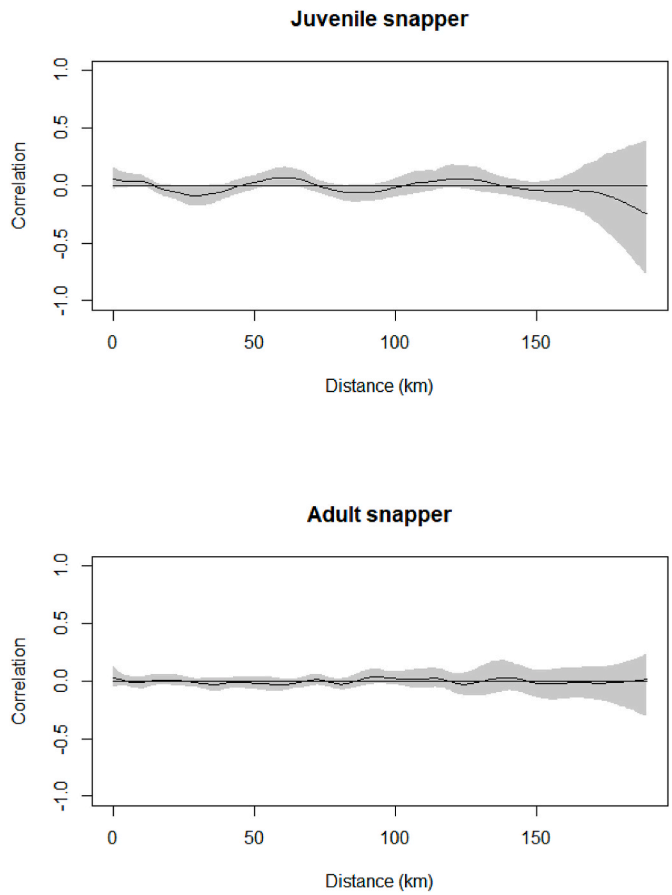

Fig. A.2. Spline correlograms examining spatial autocorrelation in the residuals of the optimal juvenile and adult snapper boosted regression trees. Shaded areas depict 95% pointwise bootstrap confidence intervals.

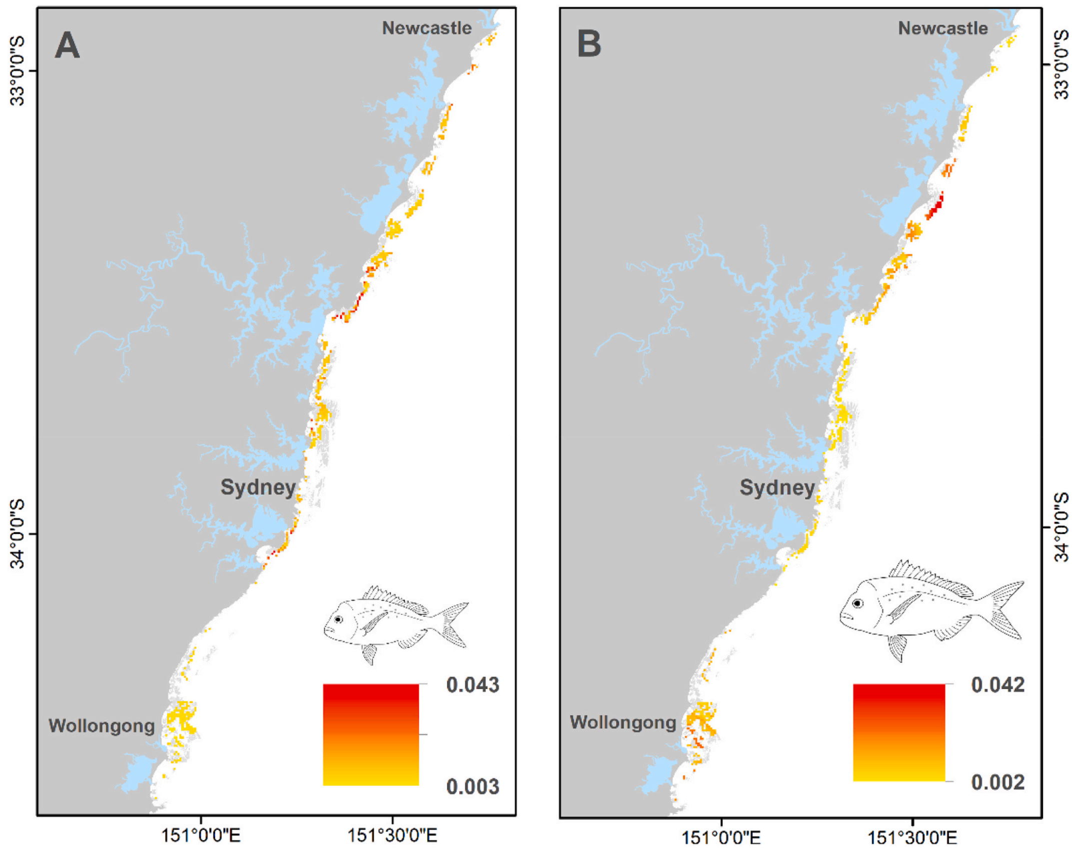

Fig. A.3. Maps of the standard deviation in mean predicted probabilities of A) juvenile and B) adult snapper from optimal boosted regression trees. The standard deviation of predictions were generated from 1000 bootstrap samples.

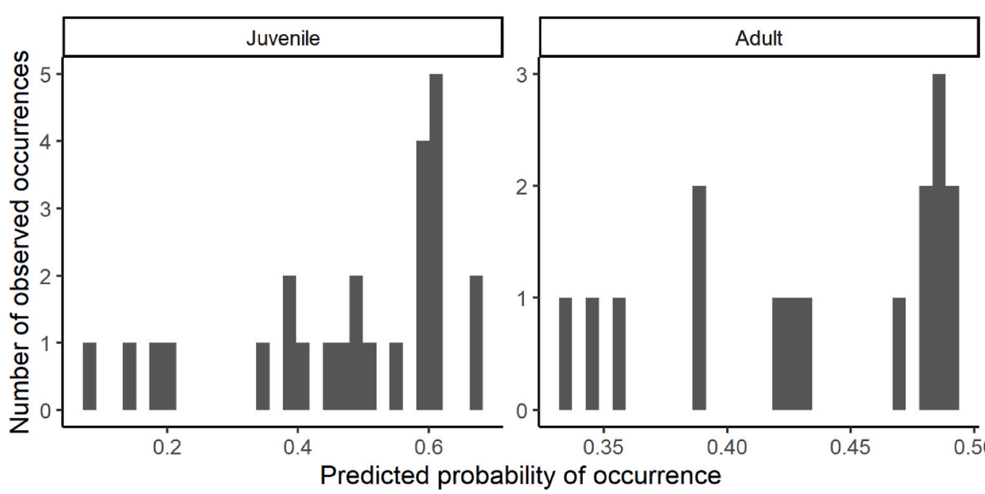

Fig. A.4. The relationship between observed probabilities of occurrence in the independent data set and predicted probabilities of occurrence from the Greater Sydney region models for A) juvenile and B) adult snapper. A higher number of observed occurrences on independent deployments predicted to have high suitability indicates reasonable reliability of the models for management purposes.

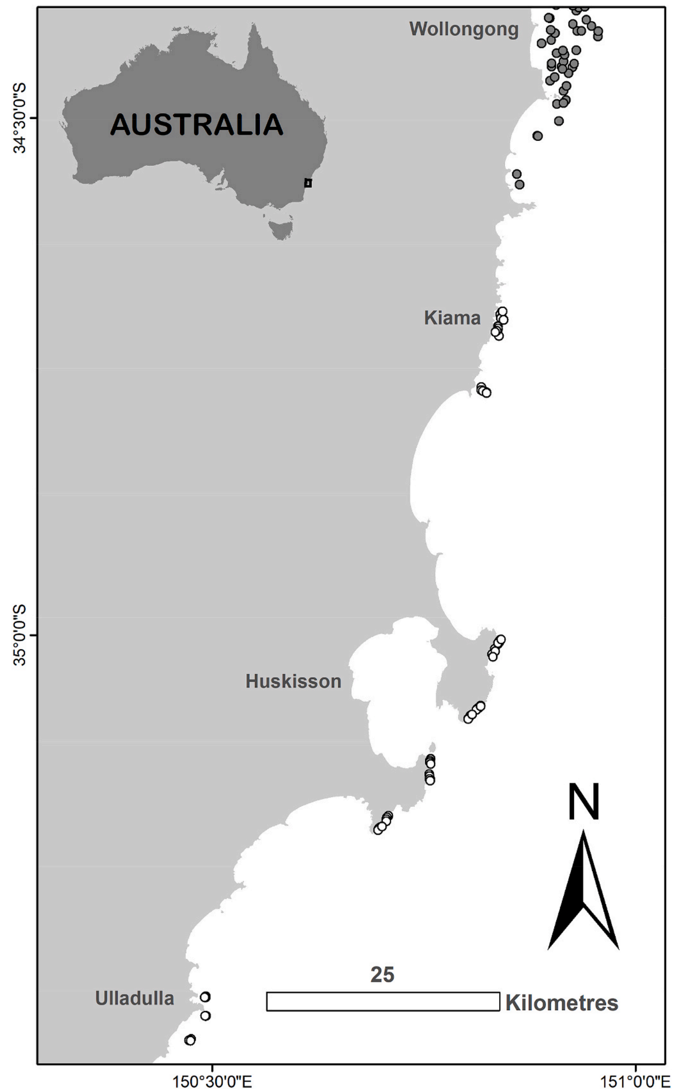

Fig. A.5. Map of the southern Greater Sydney region baited remote underwater stereo-video systems samples (grey circles) and the independent baited remote underwater stereo-video systems deployments (white circles) used for model validation.

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